



Density, occupancy, and detectability of lowland tapirs, *Tapirus terrestris*, in Vale Natural Reserve, southeastern Brazil

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The lowland tapir (*Tapirus terrestris*, Linnaeus 1758) is one of the surviving members of the Neotropical megafauna. In Brazil, lowland tapirs are considered vulnerable according to the IUCN Red List of Threatened Species and endangered within the Atlantic Rain Forest biome. We aimed to provide the 1st estimates of density and population size for *T. terrestris* for Vale Natural Reserve (VNR). We predicted the relationships of 6 covariates to habitat occupancy. Density was estimated by the use of distance-sampling techniques, while occupancy, detectability, and activity patterns were assessed with camera-trap monitoring at 39 sample sites over a 1-year period. Density for *T. terrestris* was 0.8 ± 0.2 lowland tapirs/km² and population size was 200 ± 33 individuals. Occupancy probability was described by 2 covariates (density of palm trees and distance to water resources) and detectability by those same 2 covariates plus 2 more (distance to road and density of poaching). The species showed the 3 highest peaks of activity at 1900, 2300, and 0400h. We concluded that VNR still harbors a viable population of lowland tapirs. However, anthropic impacts in the reserve such as poaching and road kills could already be directly affecting the lowland tapir population and producing indirect effects for the whole ecosystem. Results presented herein can be a starting point to support future work in the region and to make predictions regarding the ecosystem relationships, management, and conservation of lowland tapirs.

A anta brasileira (Tapirus terrestris, Linnaeus 1758) é considerada uma das espécies sobreviventes da megafauna neotropical. No Brasil, a anta é considerada vulnerável de acordo com a lista vermelha de espécies ameaçadas da IUCN e considerada em perigo para o bioma da Mata Atlântica. Nosso objetivo foi fornecer as primeiras estimativas de densidade e tamanho populacional de T. terrestris para a Reserva Natural Vale (RNV). Além disso, nós testamos o efeito de 6 covariadas para modelar ocupação do habitat. Estimamos a densidade e o tamanho populacional com a técnica de amostragem de distância por transecção linear. A detectabilidade, ocupação e período de atividade foram estimados com o uso de armadilhas fotográficas em 39 sítios amostrais por um período de 1 ano. Estimamos uma densidade de 0.8 ± 0.2 antas/km² e um tamanho populacional de 200±33 indivíduos. A probabilidade de ocupação foi representada por 2 covariadas (i.e. densidade de palmeiras e distância do recurso hídrico), e a detectabilidade pelas mesmas covariadas anteriores com a adição de outras 2 (i.e. distância da rodovia e densidade de caça). A população presente na RNV apresentou 3 picos de atividade, às 19:00, 23:00, e 04:00 horas. Nós concluímos que a RNV ainda pode apresentar uma população viável de anta. Porém, os impactos antrópicos presentes na reserva (como a caça ilegal e morte por atropelamentos) podem já estar diretamente afetando a população de anta e produzindo um efeito indireto em todo o ecossistema. Os resultados aqui apresentados podem ser o ponto inicial para o desenvolvimento de futuros estudos na região e também para predições sobre medidas de manejo e conservação da anta e de todo o ecossistema.

Key words: camera trap, distance sampling, poaching, road impact, Tapirus terrestris

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Data on how species use the habitat are necessary for understanding the ecology of each species, including spatial and temporal distributions (Gentile and Cerqueira 1995; Phillips et al. 2004), and are fundamental for management and conservation measures (Caughley 1994; Otis 1997). Each animal species is associated in different ways with structural features of their habitat (Downes et al. 1998; Tews et al. 2004); for example, the density of palms (Beck and Terbogh 2002), the presence of water resources (Goulart et al. 2009), and also elements that can be avoided by a species, for example, poaching and distance to the forest edge (Ferreguetti et al. 2015, 2016). Thus, understanding which factors determine the presence of a species in a biome as threatened as the Atlantic Rain Forest biome contributes to the development of conservation measures to ensure their survival in such areas (Jones 2001).

Lowland tapirs (*Tapirus terrestris*, Linnaeus 1758) are a surviving member of the Neotropical megafauna (Emmons and Feer 1997; Hansen and Galetti 2009; De Thoisy et al. 2010) and are distributed throughout South America, except in Chile and Uruguay (Naveda et al. 2008). In Brazil, the lowland tapir is considered vulnerable according to the IUCN Red List of Threatened Species and considered endangered in the Atlantic Rain Forest biome (Naveda et al. 2008). The lowland tapir is considered the largest terrestrial mammal occurring in Brazil, with low reproductive potential, a long gestation period, and a large home range (Eisenberg and Redford 1999). These biological aspects result in low densities (Medici 2010) and make the species relatively vulnerable to local extinctions due to demographic and environmental variations, and losses of genetic diversity (Medici et al. 2007).

The lowland tapir is still hunted for protein in most of its distribution, which represents a major threat to the species (Cullen et al. 2000; Naveda et al. 2008; Medici 2010). Studies have shown that lowland tapirs select habitat according to 2 main factors: food availability (e.g., species of palms) and water resources (Salas and Fuller 1996; Foerster and Vaughan 2002; Naranjo 2009; Medici 2010). Lowland tapirs have a home range of 1.1–14.2 km² (Medici 2011) and concentrate most of their activity in habitat patches (Tobler 2008; Medici 2010). Lowland tapirs have a low fertility rate, with a single offspring resulting after a gestation period of 13–14 months (Barongi 1993). Because of these characteristics, lowland tapirs have low abundances and are very susceptible to loss and fragmentation of habitat, poaching, road kills, and diseases transmitted by domestic animals (Naveda et al. 2008).

Although there are good data and information available on lowland tapirs, some basic knowledge still is lacking in much of its distribution. Diet, spatial and temporal distribution, intraspecific interactions, population demography, reproductive parameters, and even up-to-date presence/absence data are lacking for many localities. These very basic pieces of information are crucial for modeling the current status, viability, and risk of extinction for lowland tapir populations, as well as predicting the effects of climate change and other future scenarios. Good spatial information related to lowland tapirs and their habitats is essential for the development of these models (García et al. 2012).

To aid in the conservation of lowland tapirs, our study aimed to provide the 1st estimates of density of the species for the Vale Natural Reserve (VNR), located in the Atlantic Rain Forest biome of Brazil. By using occupancy and detectability modeling, we were able to model the spatial distribution of the species, from which we predicted the direction of response of 6 covariates based on prior knowledge of lowland tapir ecology (Eisenberg and Redford 1999; De Thoisy et al. 2010; Medici 2011; García et al. 2012). A priori, we expected that the covariates measured should represent key habitat features for the species (i.e., density of palms, distance to water resources, and tree density) or elements possibly avoided by the species (i.e., distance to road, distance to forest edge, and poaching). We tested the hypothesis that occupancy probability would be higher in sites with higher density of palms, higher density of other trees, and closeness to water resources. We also hypothesized that detectability would be higher in sites with less influence of poaching and greater distance from roads and forest edges.

MATERIALS AND METHODS

Study area.—This study was conducted in the VNR, a protected area of 235 km² belonging to the Vale Company. The reserve is located in the neighboring municipalities of Linhares and Jaguaré (19°06′–19°18′ S and 39°45′–40°19′ W), in northeastern Espírito Santo, Brazil (Fig. 1).

The VNR was established through a gradual process of land acquisition, which started in 1955, when Vale bought its 1st properties in the region, and reached its current extent in 1973. The reserve is composed of 1 main block of forest (approximately 98.1% of the total area), and a much smaller fragment, known as Biribas Reserve, to the southwest of the main block.

According to the Brazil Vegetation Map (IBGE 1993), the VNR is included within the Atlantic Rain Forest biome, composed of a mosaic of habitats with 4 main vegetation types (adapted from Jesus 1987; Peixoto and Gentry 1990): "tabuleiro" forest (coastal plain forest), riparian forest, "mussununga" forest, and natural grassland. The evergreen tabuleiro forest has 2 or more upper strata and high densities of lianas and epiphytes and covers approximately 68% of the total area of the reserve. The riparian forest, which covers some 4% of the reserve, is a mixed type of vegetation associated with streams, characterized by widely spaced trees and a predominance of palms. The mussununga forest (covering approximately 8% of the VNR) is a type of woody vegetation on sandy soils, physiognomically similar to the tabuleiro forest at an early or intermediate stage of regeneration. The natural grasslands occur as enclaves within the forest, which were once the sites of ponds in the geological past, and cover ca. 6% of the area of the reserve. In addition to these vegetation types, approximately 8% of the reserve is covered by wetlands (swamps) and streams (Fig. 1). The remaining 6% is composed of administrative structures of the reserve.

Line transect surveys.—To estimate density and abundance of *T. terrestris*, we established four 5-km long line transects in



Fig. 1.—Habitat mosaics inside the Vale Natural Reserve, Espírito Santo, Brazil. Black triangles represent the location of each camera trap, and gray lines represent survey transects.

the VNR (Karanth et al. 2004), using the RAPELD protocol (Magnusson et al. 2005). It is a technique that seeks to standardize the collection of biological data and aims to develop methods for long-term ecological research (PELD) and allow rapid inventories (Rapid Assessment Program [RAP]). Transects were separated from one other by a minimum of 4 km.

During a 13-month period (April 2013 to May 2014), transects were surveyed using distance-sampling techniques (Buckland et al. 2001). Each month, transects were surveyed twice by a single observer starting at sunrise (between 0530 and 0630h). The observer waited 3h before starting the afternoon survey, between 1300 and 1400h. The observer walked transects at a speed of approximately 1 km/h. Transects were surveyed twice per month with the order being alternated each month.

For each sighting, we recorded the perpendicular distance of the animal from the transect (measured using measuring tape), the length of transect walked to that point, date, timing of the record, and transect number. *Camera trapping.*—We selected 39 sampling sites using a systematic random design stratified by vegetation type to ensure that all 4 of the principal vegetation types found in the VNR were represented (i.e., tabuleiro, riparian, and mussununga forests, and natural grassland). This scheme was designed to model occupancy probability of the VNR by the lowland tapir, as well as document its activity pattern (Fig. 1). We placed a random grid over a digital map of the reserve and identified the sampling points by selecting grid cells.

First, in each selected grid cell, we located randomly 1 camera trap per grid cell. We did not use bait to attract lowland tapirs. This approach resulted in a relatively even distribution of points within the VNR, while maintaining independence among points, which were separated from one another by a distance of more than 1 km (Magnusson et al. 2005; Ancrenaz et al. 2012). At each site, we installed 1 passive infrared Bushnell camera trap (Bushnell Outdoor Products, Overland Park, Kansas) in picture function, approximately 40–50 cm above the ground, for continuous surveying throughout the study (from May 2013 to June 2014). All stations were examined every 20–25 days to change batteries, when necessary. Traps were programmed to operate for 24 h/day.

Covariates.—We used 6 covariates to model occupancy probability of the lowland tapir. These were distance to forest edge (edge_distance), density of trees (with a diameter at breast height [DBH] of more than 50 cm, tree_density), distance to water (water_distance), density of palms (palm_density), and distance to road (road_distance). The potential effect of poaching (poaching) on detectability and occupancy also was analyzed. A priori, these covariates were selected to represent key habitat features (palm_density, tree_density, water_distance) or elements possibly avoided by lowland tapirs (road_distance, edge_distance).

At each sampling point, we established 4 plots $(30 \times 50 \text{ m})$ arranged by the cardinal compass points (north, south, east, and west). In each plot, we measured the DBH of each tree and counted the number of large trees (DBH > 50 cm). In these plots, we also counted the number of individuals of each species of palms.

Three spatial covariates—distance to forest edge, water resource, and main road—were quantified for each of the 39 sample sites using ArcGIS software (ESRI*ArcMap 10.1, Redlands, California—ESRI 2011).

Density of poaching within the study area was calculated using the georeferenced database of a 10-year period in which poaching events were recorded by the reserve's security guards (source: VNR). The density of poaching (records per km²) was calculated for each grid cell in which a camera trap had been installed by dividing the number of records by the grid cell area.

Data analysis.—Density and population size were estimated by total number of individuals observed along each trail through the program DISTANCE 6.2 (Buckland et al. 2001). DISTANCE uses the perpendicular distances (animal-track) to estimate effective strip width (ESW) in the study area and model the detection function that best suits the probability of detection of an animal at a given distance from the track (Laake et al. 1994; Buckland et al. 2001). The best detection model was selected by the Akaike Information Criterion (AIC—Akaike 1973).

Based on an estimate of home range size of 1.1–14.2 km² for lowland tapirs (Medici 2011), we checked for spatial and temporal autocorrelation in the records of lowland tapirs for each camera trap using Mantel tests (Oksanen et al. 2012). For the Mantel tests, we calculated a spatial distance matrix using universal transverse Mercator-14 coordinates (in meters) taken at the center of each grid and a temporal distance matrix using the months of the sampling period. Euclidean distances were used to construct distance matrices for space and time. The Bray– Curtis distances were used to a construct distance matrix of the records of lowland tapir per camera. Significance of Mantel correlations were evaluated by permutation tests with 9,999 permutations. The analyses were performed in R version 2.15.0 (R Development Core Team 2012) with the package vegan version 2.0-4 for Mantel tests (Oksanen et al. 2012).

We classified camera-trapping data using 5-day intervals (27 occasions), that, based on the approach of Mackenzie et al. (2006), would be sufficient to detect or not detect lowland tapirs and constructed a reliable detection history. We estimated site occupancy (Ψ) and detection probability (p) for the species, with 3 possible outcomes: 1) the site was occupied and the species was detected ($\Psi \times p$), 2) the species was present but not detected ($\Psi \times [1 - p]$), and 3) the species was not present and not detected ($1 - \Psi$).

We estimated detection probabilities by sampling each site on 27 occasions. The probability was the parameter projected by a maximum likelihood estimation of the proportion of sites occupied (Ψ) during the sample period. We used a singleseason model. This exercise indicated that the occupancy status for tapirs was constant throughout the study, allowing closed occupancy models to be used (Mackenzie et al. 2006).

In our occupancy analysis, we assessed the covariates that might affect occupancy and detectability, in an attempt to identify habitat preferences. We constructed a set of 20 candidate models selected by a priori hypotheses based on 4 different approaches: 1) considering occupancy probability and detectability as constant across all sites, 2) considering the variation in occupancy as a function of covariates, 3) considering the variation in detectability as a function of covariates, and 4) considering both the variation in occupancy and detectability as a function of covariates. This allowed us to evaluate the differences in habitat occupancy as determined by a single covariate or a set of covariates, which would contribute to an improvement in the model's performance.

Occupancy modeling was run in PRESENCE 9.3 software (Mackenzie and Royle 2005) with 2,000 bootstraps to assess the adjustment fit (*P*) and overdispersion parameter (\hat{c}). In our assessment of occupancy closure and the factors that influenced occupancy and detection, we ranked the models by AIC adjusted for small sample size (AICc), following Burnham and Anderson (2002). All models with a Δ AICc value < 2 were considered to be competitive. We also used the AICc weight

 (w_i) for each model, which corresponds to the amount of evidence in favor of a given model, to choose the best model that we used to test our hypotheses.

The circadian cycle of the species was described based on the timing of photographs obtained from the camera traps. To avoid pseudoreplication, records were only considered to be independent when separated by an interval of 24 h. Analyses were conducted in the "Circular" package in R with associated analytic packages. Circular summaries (Lund and Agostinelli 2007) were used to determine the mean overall timing of activity as recorded by camera traps. A resampling approach was used to derive unbiased estimates of the 95% confidence intervals, whereby the circular mean from a random sample of 100 data points was calculated 10,000 times with replacement to generate reliable estimates.

RESULTS

Density and population size.—A total of 908 km of transects (196 samples) were surveyed in this study. Throughout the surveys, *T. terrestris* was sighted 63 times.

Estimated density for *T. terrestris* was 0.8 ± 0.2 lowland tapirs/km² and estimated population size was 200 ± 33 individuals with an ESW of 10.80 ± 1.12 m with observations obtained from 0 to 36 m from the line of the transect. The model that best fitted our data was a Half Normal key with cosine adjustment. The coefficient of variation for both parameters was 16.6%.

Occupancy and detectability models.—Records of the lowland tapir were not autocorrelated with respect to space (Mantel's r = -0.02, P = 0.65) or time (Mantel's r = 0.05, P = 0.23). A total of 7,020 trap-days were conducted during

the study. We obtained 2,134 independent detections of *T. terrestris* and observed the species in 30 of the 39 sites, which resulted in a naive occupancy of 0.77 and a detectability of 0.52. The northern portion of VNR resulted in the highest occupancy rates and detectability of lowland tapirs ($\Psi = 0.58$ – 0.95 and p = 0.31–0.48), followed by the southern portion ($\Psi = 0.32$ –0.43 and p = 0.18–0.29). The west portion resulted in the lowest occupancy rates and detectability ($\Psi = 0.08$ –0.13 and p = 0.06–0.09).

From the 20 occupancy models produced (Table 1), occupancy was best described by 2 covariates: 1) density of palm (palm_density), which had a positive relationship in which occupancy increased with high palm density ($\Psi = 0.11-0.98$; Fig. 2A) and 2) distance to water resources (water_distance), which had a negative relationship, in which occupancy by lowland tapirs decreased as the distance to water increased $(\Psi = 0.009-0.96;$ Fig. 2C). Detectability was affected by 4 covariates: 1) palm_density, which had a positive relationship in which detectability increased in sites with higher density of palms (p = 0.11-0.48; Fig. 2B); 2) water_distance, which had a negative relationship with higher detectability in sites with shorter distances to water (p = 0.02-0.43; Fig. 2D); 3) Density of poaching (poaching), which had a negative relationship illustrating that the higher the poaching the lower detectability (p = 0.16-0.41; Fig. 2E); and (4) distance to road (road_distance), which had a negative relationship with higher detectability in sites far away from roads (p = 0.1-0.4; Fig. 2F).

Activity pattern.— Tapirus terrestris showed a broad activity pattern, being photographed throughout the 24-h cycle (Fig. 3). The species showed 3 higher peaks of activity at 1900, 2300, and 0400 h.

Table 1.—Occupancy models for *Tapirus terrestris* in the Vale Natural Reserve, Brazil, estimated by camera trapping between May 2013 and June 2014, grouped in sampling intervals of 5 consecutive days. With (.) = as constant and covariates: distance to forest edge (edge_dist); density of trees with diameter breast height > 50 cm (tree_dens); density of poaching (poaching); density of palms (palm_dens); distance to road (road_dist); and distance to water resources (water_dist). Ψ = occupancy; *p* = detectability; overdispersion parameter (\hat{c}) = 1.14 and the adjustment fit (*P*) = 0.23.

Model	AICc	ΔAICc	W _i	Number of parameters
Ψ (palm_dens;water_dist); p (poaching;water_dist;road_dist;palm_dens)	532.62	0	0.89	8
Ψ (palm_dens;water_dist);p(poaching;road_dist;palm_dens)	540.27	7.65	0.08	7
Ψ (palm_dens;water_dist);p(poaching;water_dist;road_dist)	541.97	9.35	0.001	7
Ψ (palm_dens;water_dist);p(poaching;palm_dens)	542.01	9.39	< 0.001	6
Ψ (palm_dens);p(poaching;water_dist)	542.33	9.71	< 0.001	5
Ψ (palm_dens;water_dist);p(road_dist;palm_dens)	556.10	23.48	< 0.001	6
Ψ (palm_dens); <i>p</i> (road_dist;poaching)	556.50	23.88	< 0.001	5
Ψ (water_dist);p(road_dist;poaching)	561.14	28.52	< 0.001	5
Ψ (water_dist);p(poaching)	565.85	33.23	< 0.001	4
Ψ (palm_dens); p (poaching)	572.78	40.16	< 0.001	4
$\Psi(.);p(.)$	576.70	44.08	< 0.001	2
$\Psi(.)$; p(road_dist; poaching)	576.84	44.18	< 0.001	3
Ψ (palm_dist); $p(.)$	577.03	44.41	< 0.001	3
$\Psi(water_dist);p(.)$	577.78	45.16	< 0.001	3
$\Psi(.)$;p(poaching)	577.88	45.26	< 0.001	3
$\Psi(.); p(dist_road)$	577.98	45.36	< 0.001	3
Ψ (poaching;edge_dist); p (poaching)	578.40	45.78	< 0.001	5
$\Psi(\text{road_dist});p(.)$	578.65	46.03	< 0.001	3
$\Psi(\text{poaching});p(.)$	578.92	46.30	< 0.001	3
$\Psi(\text{edge_dist});p(.)$	579.02	46.40	< 0.001	3

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Fig. 2.—A) Relationship between occupancy of the Atlantic Rain Forest biome, Vale Natural Reserve, Espírito Santo, Brazil, by *Tapirus terrestris* and density of palms. B) Relationship between detectability of *T. terrestris* and density of palms. C) Relationship between occupancy of the Atlantic Rain Forest biome, Vale Natural Reserve, Espírito Santo, Brazil, by *T. terrestris* and distance to water resources. D) Relationship between detectability of *T. terrestris* and distance to water resources. D) Relationship between detectability of *T. terrestris* and distance to water resources. E) Relationship between detectability of *T. terrestris* in the Atlantic Rain Forest biome, Vale Natural Reserve, Espírito Santo, Brazil, and density of poaching. F) Relationship between detectability of *T. terrestris* and distance to road as estimated by camera trapping between May 2013 and June 2014, grouped in sampling intervals of 5 consecutive days.

DISCUSSION

Density and population size.—The density of lowland tapirs reported in this study, estimated using line transects in the VNR, is the 1st estimate of density for this area and showed a coefficient of variation below 20%, which is the maximum value recommended to obtain reliable estimates (Buckland et al. 2001). Thus, our density estimate serves as a starting point for monitoring the lowland tapir in the VNR and for comparison with other studies that have used the same methodology (Table 2). Density estimates for the species in the Atlantic Forest were lower than those reported in the present study. This is because those estimates were made in the fragmented areas of Morro do Diabo (0.34–0.64 individuals per km²—Medici 2010) and the Ecologic estation of Caetetus (0.47 individuals per km²—Cullen et al. 2000), both in the state of Sao Paulo. However, our estimate is similar to those obtained in more preserved areas in other biomes such as Pantanal (0.30–1.01 individuals per km²—Trolle et al. 2008) and Amazonian Forest (3.3–3.7 individuals per km²—Mendes-Pontes 2004). Those density estimates were obtained using different methodologies, which makes comparisons between studies difficult. However, herein we show that VNR contains a population of 200 ± 33



Fig. 3.—Activity pattern of *T. terrestris* in the Atlantic Rain Forest, Vale Natural Reserve, Espírito Santo, Brazil, as estimated by camera trapping between May 2013 and June 2014. Inside values 0–30 are the frequency of records and outside values are hours of the day.

lowland tapirs, which may be considered a viable population for conservation (Gatti et al. 2011).

Occupancy and detectability models.—The model to predict potential habitat suitability for lowland tapirs in the VNR showed that among the 6 covariates evaluated in this study, 2 best explained habitat occupancy by lowland tapirs (i.e., distance to water resources and density of palms) and 4 were best able to predict detectability for the species (i.e., density of palms, distance to water resources, poaching, and distance to road).

The relationship between occupancy by lowland tapirs and distance to water resources was expected after it was determined which habitats they usually occupied, such as riparian forests, wetlands, and streams, where they are most active, especially when foraging (Medici 2010), making it easy to detect individuals in sites closest to a water resource. Thus, the highest occupancy rates and detectability of the lowland tapir in the northern portion of the VNR can be attributed to this portion of the reserve having a higher quantity of water resources (Kierulff et al. 2015) compared to the other portions of VNR (i.e., south and west). Norris (2014) found that distance to water was one of the covariates that best described the distribution of lowland tapirs. Lowland tapirs also used sites closest to water as a place for resting, defecation, to prevent ectoparasites, to facilitate their movements between foraging sites, and for cooling off during the hottest hours of the day (Padilla and Dowler 1994; Foerster and Vaughan 2002). Brazil currently is experiencing a hydro crisis that began in 2014. Lack of rainfall (CPTEC 2015), along with the creation of artificial barrages to store water, has damaged ecosystems and animal populations, especially species like the lowland tapir which is highly dependent on water (García et al. 2012). Many streams are disappearing because of this process.

Along with water resources, the density of palms is also a covariate that represents a habitat key to the lowland tapir, because the fruits produced by these palm trees are crucial food

Table 2.—Density estimates of *Tapirus terrestris* per km^2 in the Brazilian biomes. FIT = Footprint Identification Technique; ind = individuals.

Biome	Location	Density (ind/km ²)	Reference and applied method	
Atlantic Forest	Ecologic Estation Caetetús, São Paulo	0.47	Cullen et al. (2000), line transect	
Atlantic Forest	State Park Morro do Diabo, São Paulo	0.20-0.84	Cullen et al. (2000), line transect	
Atlantic Forest	Fazenda Mosquito, São Paulo	0.3	Cullen et al. (2000), line transect	
Atlantic Forest	State Park Mata dos Godoy, Paraná	2.20-2.50	Rocha (2001), number of observations/area	
Atlantic Forest	State Park Morro do Diabo, São Paulo	0.43	Medici (2010), FIT	
Atlantic Forest	State Park Morro do Diabo, São Paulo	0.64	Medici (2010), line transect	
Atlantic Forest	State Park Morro do Diabo, São Paulo	0.34	Medici (2010), radiotelemetry	
Atlantic Forest	Caraguatatuba, São Paulo	0.13-0.21	Ramírez (2013), genetic analysis	
Atlantic Forest	Intervales, São Paulo	0.20-0.57	Ramírez (2013), genetic analysis	
Atlantic Forest	Vale Natural Reserve, Espírito Santo	0.6–1.0	Present study, line transect	
Amazon Forest	Brazilian Amazon	0.11-0.52	Peres (2000), line transect	
Amazon Forest	Center of ecological studies Kayapó, Para	0.62	Zimmerman et al. (2001), line transect	
Amazon Forest	Ecological Estation of Maracá, Roraima	3.3–3.7	Mendes-Pontes (2004), line transect	
Amazon Forest	Lake Uauaçú, Mid-West Amazon	0.23	Haugaasen and Peres (2005), line transect	
Pantanal	Fazenda Acurizal, Paraguay River	0.64	Schaller (1983), direct counts	
Pantanal	Fazenda Nhumirim, Nhecolândia	Forest: 0.40; Cerrado: 0.13	Desbiez (2007) and Desbiez (2009), line transect	
Pantanal	SESC Pantanal, Barão de Melgaço	Forest: 0.71; open areas: 0.37	Cordeiro (2004), line transect	
Pantanal	SESC Pantanal, Barão de Melgaço	0.47-0.69	Trolle et al. (2008), camera trap	
Pantanal	SESC Pantanal, Barão de Melgaço	0.30-1.01	Trolle et al. (2008), line transect	

Downloaded from https://academic.oup.com/jmammal/article-abstract/98/1/114/2977226/Density-occupancy-and-detectability-of-lowland by University of Texas at Austin user on 04 September 2017 resources for lowland tapirs (Fragoso 1997). The northern part of the reserve had the highest occupancy rates and palm density values, which were expected as much of the riparian forests (i.e., vegetation type that presents high dominance of palm trees) are located in the northern VNR (Kierulff et al. 2015). In the Atlantic Rain Forest biome of Brazil, lowland tapirs are known to use patches of Jerivá palm (*Syagrus romanzoffiana*) very intensively (Galetti et al. 2001; Tófoli 2006). In the northeastern region of the Brazilian Pantanal, lowland tapirs show a high preference for Acuri palm forests (*Attalea phalerata*) compared to other vegetation types (Cordeiro 2004). In the Amazon, patches of *Mauritia flexuosa* frequently are visited by lowland tapirs (Bodmer 1990; Tobler 2008). Accordingly, occupancy and detectability models demonstrate high occurrence probabilities in such habitat areas.

Besides natural habitat factors, anthropic factors (i.e., poaching and roads) potentially could influence the detectability of lowland tapirs (Licona et al. 2011). Poaching was reported as a problem for animal populations in VNR since 1999 (Chiarello 2000) and the west portion of the VNR is the most affected by poaching (Kierulff et al. 2015). The high rate of poaching in the western portion of the VNR was associated with the lowest occupancy rates and detectability of lowland tapirs. The detectability of lowland tapirs has likely been affected by poaching as it is known that tapirs tend to avoid areas with higher hunting activity (Laundre et al. 2010). Medici et al. (2007) conducted a population and habitat viability analysis for lowland tapirs and found that poaching is one of the major threats to the species, which is consistent with previous research where the presence of lowland tapirs and the level of poaching were negatively correlated (Peres 2000; Cullen et al. 2001; Fa et al. 2002; Cruz et al. 2014). Lowland tapirs especially are vulnerable to hunting when compared with other ungulates (e.g., cervids-Ferreguetti et al. 2015) because of their relatively low-density population (Bodmer et al. 1997; Medici et al. 2007) and life history traits (i.e., long-lived individuals, low rates of increase, and long generation times-Bodmer et al. 1997; Emmons and Feer 1997). Poaching not only has a negative effect on lowland tapir populations, but also has an indirect effect on the composition and structure of the forest, because lowland tapirs play a critical ecological role, affecting the structure, composition, growth, and regeneration of vegetation (Bodmer 1990, 1991; Dirzo and Miranda 1991; Fragoso 1997; Galetti et al. 2015).

Detectability was lowest in sites closest to the road that cuts the VNR, suggesting that lowland tapirs could be avoiding areas next to roads. Roads and other human developments may act as barriers, because the animals tend to avoid sites closest to roads, a behavior that has been reported for other large mammals occurring in contiguous habitats (Paetkau et al. 1997). Combined with our finding that detectability is lower in sites closest to the road, during the period of June 2014 to June 2015, 4 individuals of lowland tapir were found dead in the road that cuts the reserve (i.e., BR 101 road), and 1 of the individuals was a pregnant female. To maintain the flow of lowland tapirs across roads, construction of special structures such as wildlife crossings have been proposed (Foster and Humphrey 1995). For example, in Alberta, Canada, the construction of these structures favored the passage of large mammals such as bears (*Ursus arctos*), wolves (*Canis lupus*), moose (*Cervus elaphus*), and deer (*Odocoileus* sp.) along the Trans-Canada highway (Clevenger and Waltho 2005).

Activity period.—Lowland tapirs have been described as nocturnal or crepuscular (Padilla and Dowler 1994; Noss et al. 2003; Tobler 2008; Medici 2010; Wallace et al. 2012; Cruz et al. 2014); however, several factors can affect the activity period of this species (i.e., poaching, rainy season). For lowland tapirs, increased diurnal activity was observed in humid months (Foerster and Vaughan 2002; Medici 2010). Lowland tapirs usually are inactive in the middle of the day, which corresponds to the hottest hours of the day (Medici 2010). From personal observation, we noticed that during the hottest hours of the line transect survey, lowland tapirs were found bedded down in the forest interior.

Implications for conservation.—Although the present study was conducted in the VNR, the northern region of the state of Espírito Santo holds a connected block of protected area of 550 km². This protected block has 2 important purposes: 1) monitoring the lowland tapir population in the state of Espírito Santo, and 2) quantifying the impact of roads on animal populations. Results presented herein can be a starting point to support future work in the region and to make predictions regarding the ecosystem relationships, management, and conservation of lowland tapirs. Furthermore, the results can be used as a surrogate for other regions or biomes in which the species occurs, because many locations may be affected by the same covariates used herein (i.e., poaching and road impact).

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